Crop vegetation structure is more important than crop type in determining where Lesser Kestrel's forage

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Summary

We studied foraging habitat selection by Lesser Kestrels throughout the breeding period in South-Western Spain by means of transects in which foraging observations were recorded. We focused on the effect of habitat and crop type, but also on the effect of vegetation structure and the presence of agricultural activities in the field on Lesser Kestrel's use. We considered both the accumulated use of the foraging area during the breeding season and the instantaneous foraging habitat selection by kestrels. Foraging habitat selection was highly dynamic following crop development and agricultural activities. Almost all major arable crop types showed positive selection during some part of the breeding cycle. Accumulated use by kestrels demonstrated positive associations with wheat and cotton fields and negative selection of permanent habitat types, such as forested areas, woody crops and built-up areas that have no prey or are not used by the species due to unfavourable structure. Vegetation structure appears to play a major role in instantaneous foraging selection. Lesser Kestrels select fields with short vegetation and intermediate cover. They also forage on field margins, and where agricultural activities like ploughing or harvesting, that facilitate access to prey, are being conducted. Our results help to clarify apparent controversies among previous studies on the subject, highlighting the importance of the heterogeneity of agricultural landscapes around colonies (crops in different growth stages which provide variable vegetation height and cover during the breeding cycle) and the effect that agricultural activities have on facilitating access to prey. Beyond the species-specific approach, our work encourages further studies on habitat selection by farmland birds to account not only for human-based categorization of habitats (e.g. crop type) but also on objective measures such as vegetation height and cover that influence access to prey and better reflect the high dynamism of agricultural landscapes.

Key-words: agro-environmental schemes, farmlands, Lesser Kestrel, management

Resumen

Se estudió la selección del hábitat de caza del cernícalo primilla a lo largo del ciclo reproductivo en el suroeste de España mediante transectos en los que se registró el comportamiento de los individuos observados. Se evaluó el efecto de los usos del suelo, tipo de cultivo, estructura de la vegetación y presencia de actividades agrícolas en el uso acumulado y la selección instantánea del hábitat de caza de los cernícalos. La selección del hábitat de caza demostró ser muy dinámica en función del desarrollo de los cultivos y las actividades agrícolas. Casi todos los cultivos herbáceos mostraron una selección positiva por parte de los cernícalos en algún momento del ciclo reproductivo. El uso acumulado mostró relaciones positivas con el trigo y el algodón y una selección negativa de hábitats o cultivos permanentes que o bien son pobres en presas o son rechazados por la especie por su estructura, como las áreas forestales, los cultivos leñosos o las zonas urbanas. La estructura de la vegetación parece que juega un papel preponderante en la selección instantánea del hábitat de caza. Los cernícalos seleccionaron áreas con vegetación baja y con cobertura intermedia. También cazaron sobre lindes y allí donde se estaban llevando a cabo actividades agrícolas, como el arado o el cosechado, que facilitan el acceso a las presas. Nuestros resultados contribuyen a esclarecer las aparentes controversias entre estudios previos, subrayando la importancia de la heterogeneidad del paisaje agrícola alrededor de las colonias (cultivos en diferentes estados de crecimiento que ofrecen variabilidad en la altura de la vegetación y cobertura a lo largo de todo el ciclo reproductivo) así como el efecto de las actividades agrícolas que podrían estar facilitando el acceso a las presas por parte de los cernícalos. Más allá de la aproximación específica, nuestro trabajo incentiva la utilización de variables objetivas como la altura y la cobertura de la vegetación --en

lugar de clasificaciones de interés humano como el tipo de cultivo-- que reflejan mejor la disponibilidad de presas y el gran dinamismo estructural de los paisajes agrícolas.

Introduction

Studies on wildlife habitat selection constitute a basic element in conservation and management plans (Morrison et al. 1998, Sutherland and Green 2004). The assumption underlying these plans is that species will reproduce or survive better in preferred habitats (Morrison et al. 1998). This is especially true for foraging habitats, whose quality greatly influences both adult survival and breeding success (Janes 1985).

After millennia of agricultural expansion, a high proportion of Europe's biodiversity now survives on land dedicated to food production (Krebs et al. 1999). Thus, farmlands constitute the foraging and breeding habitat of many species (Tucker and Evans 1997). In Southern Europe, a sizable part of this habitat was extensively cultivated in a traditional rotational system that resulted in patches of cereal, fallow, ploughed and stubble fields (Suárez et al. 1997). Despite their artificial nature, these so-called pseudo-steppes support a high number of bird species with an unfavourable conservation status in Europe (Tucker 1997, Tucker and Evans 1997). Due to its marginal yields, however, pseudo-steppes have undergone a transformation towards intensive agriculture with an increase of irrigated cultures in more productive areas and afforestation or abandonment in less productive ones (Tucker and Heath 1994, Suárez et al. 1997, Tucker and Evans 1997). These land-use changes have been related to the decline of both threatened steppe species and farmland biodiversity in Europe (Ormerod et al. 2003, Silva et al. 2004, Alonso et al. 2005).

One species showing a dramatic decline in conjunction with the transformation of pseudo-steppes has been the Lesser Kestrel *Falco naumanni* (Donázar et al. 1993, Tucker and Heath 1994, Bustamante 1997, Tella et al. 1998). The Lesser Kestrel is a small insectivorous falcon that inhabits open and cultivated landscapes in the Palaearctic region and over-winters in Africa. The species is colonial, often nesting in holes and crevices of cliffs; however, most breeding colonies in South-western Europe are located in large urban buildings (such as churches and castles) and farms houses in the countryside (Negro 1997, Ferguson-Lees and Christie 2004). Previous studies have shown that the species is positively associated with cereal-dominated, extensively cultivated landscapes, which also provide fallows and patches of semi-natural habitat (Bustamante 1997, Franco et al. 2004, García et al. 2006). Semi-natural habitats and field margins are preferred foraging places (Donázar et al. 1993, Franco et al. 2004, García et al. 2006, Tella et al. 1998) given the higher prey density of these areas (Rodríguez and Bustamante 2008). The reduction in both the extent and quality of these foraging habitats in its Western Palearctic breeding range appears to be the primary cause of decline of the Lesser Kestrel (Peet and Gallo-Orsi 2000, Ferguson-Lees and Christie 2004).

Beyond these generalities, previous studies do not completely agree as to the foraging habitat selection by the species, especially at the level of crop type (see Donázar et al. 1993, Franco et al. 2004, García et al. 2006, Tella et al. 1998, Ursua et al. 2005, De Frutos et al. 2010). For instance, cereal crops that constitute the main agricultural land-use throughout the Lesser Kestrel breeding range in Western Europe have been reported to be both avoided (García et al. 2006) and selected by the species (Donazar et al. 1993, Tella et al. 1998). Previous studies on Lesser Kestrel foraging habitat selection comprise a set of local truths that makes it difficult to establish species management recommendations. This is due in part to the fact that some of these studies only focused on a particular period within the breeding season, whereas others considered the breeding season as a whole. The number of land-uses and crop types, as well as the degree of agricultural intensification, also varies among study areas. Finally, the dynamic nature of crop development and Lesser Kestrel phenology may also partly explain this apparent controversy. Foraging demands and constraints of breeding kestrels change throughout the breeding season. For example, during courtship males feed females which must gain weight in preparation for egg laying (Donazar et al. 1992); while during incubation, one member of the pair must incubate the eggs, reducing the time available for foraging. However, during the nestling period food requirements dramatically increase forcing both parents to forage from dawn to dusk. Likewise, crop development shows dramatic changes throughout the Lesser Kestrel breeding season (Figure 1). For instance, sunflower (*Helianthus annuus*) plants are sown in March and then gradually develop until reaching a height of 1.5m in June-July; and this development is expected to influence Lesser Kestrel foraging via prey availability and accessibility.

{Suggested position of Figure 1}

For these reasons, our goal was to assess Lesser Kestrel foraging habitat preferences during the breeding season from different temporal perspectives, ranging from accumulated use to instantaneous foraging habitat selection. From the perspective of accumulated use, we aimed to evaluate the average suitability of different crop types, independently of kestrel and crop phenologies. We also evaluated the Lesser Kestrel's selectivity of different crop types during the three main periods within the breeding season: courtship, incubation and nestling. From the instantaneous foraging habitat selection perspective, we assessed the effects of crop type, crop development stage, vegetation structure, and agricultural activities on Lesser Kestrel foraging decisions.

Methods

Study area

The study was conducted in La Palma del Condado (Huelva, Spain) where a colony of around 25-30 Lesser Kestrel breeding pairs, located in a building holding a grain silo, has been studied since 1997 (see Rodriguez and Bustamante 2003 for details). The study area is in the flat alluvial plain of the Guadalquivir river (elevation range 20-240 m), which is dominated by agricultural fields and has little natural vegetation (primarily open holm oak *Quercus ilex* woodland; Fernández et al. 1992). The study area consists of an agricultural mosaic dominated by dry agriculture with small fields of around 0.34 ha. The main crop types are wheat *Triticum* ssp, sunflower and cotton *Gossypium* ssp, all of which show different phenologies (Figure 1). Vineyards (*Vitis vinifera*), olive (*Olea europaea*) and orange (*Citrus x sinensis*) groves and forested areas occupy a small extent. Annual mean precipitation is approximately 600 mm and the annual mean temperature is 19 ºC.

Field procedures

Fieldwork was conducted from the first week of March to last week of July 2007. Six transects were defined to homogeneously cover a circle with a 4 km radius surrounding the colony (Figure 2). Previous studies have found that kestrels mainly forage within this distance from the colony during the breeding season (Negro et al. 1991, Franco and Sutherland, 2004). Transects were designed as closed loops starting at the village of La Palma del Condado given the radial configuration of the network of unpaved roads in the area and logistic constraints (to maximize the time spent surveying versus movement between different transects). Transects were performed on bicycle by a single observer (E.R.) along unpaved roads at a constant speed (around 5 km/h), between 2 hours after sunrise and 2 hours before sunset (Andersen 2007). We selected days with good visibility, low wind (<13-19 km/h), and no rainfall. The six transects were visited weekly. In order to avoid sampling biases, the starting point within the transect, start time, and direction of movement were selected at random for each visit. Each time a single kestrel or flock was detected the observer stopped, selected a focal bird and recorded its position using GPS (Thales – MobileMapper CE) with ± 5m accuracy, and the distance and angle to the bird using a high precision rangefinder (Leica – Laser Locator 1.0; distance: ± 1m < 1000m; Compass ± 0.5º). This procedure allowed us to determine the accurate location of each focal bird and then assign the observation to a habitat type using GIS of the study area. The observer recorded the sex and age of the focal Lesser Kestrel, assigning a different ID to each individual. The observer also recorded the focal bird's behaviour for five minutes, until a prey item was captured, or until visual contact was lost because the bird left the area. Focal bird behaviour was recorded as making a strike (when the kestrel dived to the ground to capture a prey), hunting (when actively prospecting for prey on the wing or from a perch but no strikes were recorded), or engaged in other activities (resting, flying, fighting, etc.). Observation was timed from the moment the bird was detected until it made a strike, and until it made a successful prey capture. Data were recorded using a PDA with the free software Cybertracker (www.cybertracker.co.za). Changes in foraging habitat or behaviour were registered as separate events and the new position of the bird was determined (but records were attributed to the same individual). Each time a bird was recorded as hunting or making a strike the observer documented the habitat type where it took place (as well as whether the field appeared recently ploughed, sown or harvested), vegetation height and vegetation ground cover, and the simultaneous presence of agricultural activities in the field. Crop height and ground cover were categorized. For crop height we used body references: ankle, knee, waist, shoulder, head and higher (later translated into cm). For crop cover, we used six categories ranging from bare ground (including ploughed) to complete ground cover (see Table S1 for details).

{Suggested position of Figure 2}

Land-use quantification

A GIS of the study area was built using Arc-view 3.2. Field limits were extracted from 1:10,000 digital maps of the study area (Junta de Andalucía 2007) and soil occupation of each field along transects was collected monthly by field visits, recording habitat type, vegetation height and vegetation cover. We also considered temporal stages of crops such as ploughed, sown or harvested. Sampling cells for Lesser Kestrel use were defined by overlaying a 250 x 250 m grid on the study area. We included in our survey the 726 cells with > 75% of its surface inside a 700 m-wide buffer along both sides of the transects. A distance of 700 m was selected because all first contacts with kestrels were less than 700 m from the transects. Because information on habitat type was gathered on a field basis, we used SIG software to calculate the percentage of the different habitat types for each surveyed cell (see Table S2). This software also allows for the quantification of the length (in m) of linear elements inside each cell. Unfortunately, we could not quantify the relative contribution of different elements (paved and unpaved roads, field margins, or water courses) to this measure. The Pielou evenness index (J'; Pielou 1966), and the distance from transect to the centroid of each cell were also calculated.

Statistical analyses

We graphically explored the data to visualize the patterns of response variables (type of use by Lesser Kestrels) in relation to explanatory variables using basic statistics such as Wilcoxon rank sum test to quantify the differences (see Table S2). Minor uses with similar impact on lesser kestrel foraging were further grouped to simplify analyses.

We analyzed data following three different approaches that considered different temporal and spatial resolutions (Table S3).

1) Temporal changes in habitat use vs. availability during the periods of courtship (March and April), incubation (May) and nestling (June and July). For each of these periods, we calculated the Savage Selectivity Index (SSI hereafter), which has been previously applied in similar studies (Tella and Forero 2000; García et al. 2006). The SSI is calculated following the equation: $W_i = U_i/pi$, where U_i is the proportion of birds observed in hunting behaviour in habitat *i* and p_i is the proportion of that habitat at that particular time, according to monthly surveys. The SSI index ranges from 0 (maximum negative selection) to infinity (maximum positive selection), 1 indicating no selection. In order to test the null hypothesis that birds use a foraging habitat in proportion to its availability, we compared the statistic $(Wi\text{-}1)^2/\text{S.E.}(Wi)^2$ with the critical value of a Chi-square distribution with one degree of freedom. The Standard error of the index (S.E.) was calculated as $\sqrt{(1\text{-}p_i/u \text{ x } p_i)}$, where *u* is the total number of foraging records (Manly et al. 1993, Tella and Forero 2000, García et al. 2006). We carried out the analyses on the basis of habitat type proportion in each breeding period, considering temporal stages of the field, such as ploughed, whose availability change from one period to the next. All comparisons were corrected for multiple tests using the Bonferroni criteria. For calculating *Wi*, we only used the first record of each hunting individual (N = 200). Further observations of the same individual were not considered to avoid pseudoreplication.

2) Accumulated use from March to July: we integrated information on habitat types, considering the crop type to which the field was ultimately devoted (e.g. a cotton field was considered as “cotton” despite that for half of the study period it was ploughed). As some fields were regularly ploughed during the whole study period, to avoid confusion with those ploughed and planted with crops, we used the term “permanently ploughed” to refer to the former. Regarding Lesser Kestrel use, we only

used the first record of each hunting individual (N = 200) to prevent pseudoreplication. Cells were classified hierarchically depending on the kind of accumulated kestrel use that we recorded within the cell for the whole period (from March to July). Specifically, those in which kestrels were observed at least once were classified as “Presence Cells”; within these cells, those in which kestrels were observed hunting were classified as “Hunting Cells”; and within these, those in which kestrels were observed diving for prey were classified as “Strike Cells” (scheme and sample sizes in Fig. 3). We also recorded for each cell the number of strikes that resulted in a prey capture (N = 98) compared with the number of strikes that resulted in failure (N = 44; note that more than 1 strike per cell could be recorded).

With this information we built nested datasets for the analysis of different response variables. First, using all cells we built models to explain presence/absence of kestrels. On the subset of “Presence Cells”, we built models to explain presence/absence of “hunting activity”. On the subset of “Hunting Cells” we then built models to explain the presence/absence of “strikes”. And finally, on the subset of “Strike Cells” we built models to explain the ratio between successful prey capture and failure (Fig. 3)

{Suggested position of Figure 3}

We used the step.gam procedure of the gam package of R (R Development Core Team 2010), which uses a forward-backward stepwise procedure, to fit generalized additive models (Hastie and Tibshiriani 1990) to each subset of data using a binomial error and logit link. The step.gam procedure uses a stepwise search to select the best model in terms of Akaike’s Information Criterion (AIC; Akaike 1974), which takes into account both the information explained by the model and its complexity (the lower the AIC, the better the model, Sakamoto et al. 1986). The distance from the transect to each cell was included initially in the models as a correction factor, given that the probability of contact with a kestrel decreases with distance from a transect. This correction is better than using an offset, as the effect of this variable in the detection function is estimated from the data. Models were fitted by following two strategies. First, all potential predictors were sequentially tested as a smooth spline with 3 d.f. to improve the null model and the best predictor was included. A smooth spline was used because we expected nonlinear relationships between some predictors and kestrel use. The procedure continued, attempting to lower the d.f. of the spline or to include new predictors in the model, until no spline could be simplified or no extra predictors entered the model. Second, all potential predictors were sequentially tested initially as linear terms to improve the null model and the best predictor was included. The procedure continued to test whether the relationship with the predictor could be improved by using a spline with 2 or 3 d.f., or by including new linear predictors. The procedure ended when no additional predictors entered the model or the relationship could not be improved by using splines. Each of these strategies resulted in a minimum adequate model for each response variable.

3) Instantaneous foraging habitat selection was analyzed using all contacts with lesser kestrels engaged in hunting activity (416 observations for 202 individuals) by means of generalized linear mixed-effects models (GLMMs), using the lme4 package of the R software (R Development Core Team 2010). All observations were used introducing individual ID as a random factor in the analyses to avoid pseudoreplication. We analyzed, as binomial variables, whether or not contact with a kestrel engaged in hunting activity ended with a strike (1/0) and whether or not the strike (N = 136) was successful (1/0). As potential predictors we considered phenology (a factor with three levels: courtship, incubation and nestling period), habitat type, vegetation height (semi-continuous variable with 6 levels; see methods), vegetation cover (semi-continuous

variable with 6 levels) and presence of agricultural activities in the field (mainly ploughing, sowing and harvesting) while observation was recorded. We started from a full model that was manually simplified using AIC as criterion for model selection. AIC of models explored are provided in supplementary material.

Results

Transects were surveyed for a total of 138 hours resulting in 620 contacts with individuals or groups of Lesser Kestrels from which 416 were individuals engaged in hunting activity. These contacts correspond to 202 independent hunting sequences on 37 different days. Lesser Kestrels spent on average 1.95 (± 0.13) min from the time of contact to first strike and 2.25 (± 0.22) min to prey capture. Average success rate was 68% and kestrels made a strike every 21 seconds of observed hunting activity.

Temporal changes in habitat use vs. availability

The SSI demonstrated different habitat selection by Lesser Kestrels depending on the breeding period (Table 1). During courtship (61 observations), ploughed fields were selected significantly more than expected according to their availability. During incubation (32 observations), kestrels showed a positive selection for ploughed fields and fields of developing sunflowers. During the nestling period (107 observations), kestrels positively selected cereal and beetroot fields that were being harvested at that time, as well as cotton fields, starting to grown and with low vegetation cover (Table 1). We did not record hunting kestrels in either built-up areas or woody vegetation although they represent more than 20% of the land-use around the colony (Table 1).

{Suggested position of Table 1}

Accumulated use from March to July

The two final models for Lesser Kestrel presence included a negative relationship with distance from transect (correction factor), distance to colony, proportion of forested areas, fruit trees and vineyards (FFV) and proportion of built-up, water, and unproductive land (BWU). Conversely, cover of wheat, cotton, beetroot and permanently ploughed fields showed a positive impact on Lesser Kestrel presence. The proportion of beetroot and permanently ploughed fields showed a quadratic pattern with an optimum around 30% of cell cover. The model starting with linear terms (Fig 4. Plot a) additionally included the negative impact of linear elements. In this model, wheat entered as a linear term, while in the alternative model it showed a non-linear shape (Fig 4. Plot b). According to AIC, model a is better than model b (Table S4).

{Suggested position of Figure 4}

Models attempting to explain whether kestrels are hunting, whether they strike and strike success were much less informative than models for Lesser Kestrel presence, primarily reporting the negative impact of some variables already included in models for Lesser Kestrel presence (Tables S5, S6, S7 in appendix; see also Table S2).

Instantaneous foraging habitat selection

Using the hunting sequence as the sampling unit, and GLMM models to avoid pseudoreplication, we found that Lesser Kestrels preferred to strike in places with short vegetation (shorter than in neighbouring fields) but some vegetation cover (Table 2). When vegetation cover was transformed into a factor with two levels, namely bare ground vs. vegetated, the effect was similar on Lesser Kestrel strikes and the resulting model was the best according to AIC (Table 2; model 2). AIC values of models explored are provided in supplementary material.

{Suggested position of Table 2}

Strike success rate was influenced by phenology (highest during incubation, followed by nestling and then courtship) and habitat type (higher in field margins) and facilitated by agricultural activities conducted in the field (ploughing, sowing or harvesting had a positive impact on success rate; Table 3). Since parameter estimates for all habitat types except for field margins were very similar (Table S8), we simplified this variable into a binary variable: margin/no margin. Vegetation height and cover that were present in the preliminary model (Table S8) were no longer significant. AIC values of models explored are provided in supplementary material.

{Suggested position of Table 3}

Discussion

The three different analytical approaches used in this study allow us to evaluate the effect of crop types, agricultural activities (ploughing, sowing or harvesting) and vegetation structure (vegetation height and cover) on the foraging habitat selection of the Lesser Kestrel. This analysis provides a better understanding of the effects of habitat type and agricultural practices on Lesser Kestrel's foraging activity and may help clarify apparent controversies among previous studies on the subject.

Our results demonstrate both the clear preference of Lesser Kestrels for foraging in herbaceous habitats, and the rejection of permanent habitats such as olive groves, orange groves, fruit orchards and vineyards. Accumulated hunting activity also shows a preference for foraging in close proximity to the colony. In this respect, our results are consistent with the findings of previous studies (Donazar et al. 1993, Franco and Sutherland 2004, García et al. 2006). However, our approach is novel in that we consider habitat selection at different temporal scales. Although Lesser Kestrels showed no clear preference for specific arable crops in our study area when the breeding season was considered as a whole, values for the selectivity index calculated for courtship, incubation and nestling periods indicate that all major arable crops in the area (wheat, sunflower, cotton and beetroot) are positively selected by kestrels during at least one of the periods analyzed. This highlights the importance of considering phenology when studying foraging habitat selection in farmed landscapes.

The fact that models for hunting, strikes and strike success were less predictive than models for Lesser Kestrel presence (and included primarily as predictors a negative relationship with rejected habitats such as woody vegetation and built-up areas) may be partly due to the decreasing sample size of these data sets; but also may be indicative of kestrels spending most of the time out of the colony engaged in hunting activity (thus differences between presence and hunting are small; see Table S2). They also fly high when commuting from the colony (authors unpub. data) so they are only observed in favourable hunting habitats. Although we expected a positive effect of linear elements on Lesser Kestrel presence, given that they provide information regarding habitat fragmentation and the availability of field margins, this variable is also accounting for limits of built-up areas that have a negative impact on kestrels.

At the level of instantaneous foraging, or habitat selection derived from individual foraging sequences, we found that kestrels select field margins (where prey find refuge) and that foraging habitat selection and hunting success are greatly affected by factors that change dynamically during the breeding cycle such as crop phenology and agricultural activities. Vegetation height is of crucial importance to foraging kestrels (Table 2), as was found in other studies on the species (Franco and Sutherland 2004, Franco et al. 2004, García et al. 2006) and other raptors (Shrubb 1980, Toland 1987, Ontiveros et al. 2005, Tapia et al. 2007). The presence of short vegetation probably determines the shorter time needed by Lesser Kestrels to make a strike and the higher hunting success rate compared with more vegetated areas (see Tella et al. 1998). The positive selection of ploughed fields according to the SSI during different periods of the breeding cycle is consistent with the Lesser Kestrel preference for low vegetation height, although the negative impact of bare ground suggests that some vegetation should remain or start growing (recently sown) in these fields. Due to the high dynamism of agricultural ecosystems, however, both the relative availability of areas with low vegetation height and their composition (crop types) dramatically change during the breeding season, thus explaining differences in selectivity among periods and the importance of the variable “phenological period” in the mixed models (Table 3). In March, the area is a mixture of green cereal, fallows and ploughed fields (some of them already sown). Therefore, the availability of fields with low vegetation height reaches a maximum at this time and, as suggested by models for successful strikes and the selectivity index, kestrels may profit from ploughing and sowing activities because they improve accessibility to fossorial species such as earthworms, field crickets and the mole cricket (*Gryllotalpa gryllotalpa*), which has been found to be preferentially consumed during courtship and incubation periods (Choisy et al. 1999, Rodriguez et al. 2010, Catry et al. 2012a). The reported avoidance of ploughed fields (Ursúa et al. 2005) or their use in accordance with their availability in other areas (Tella et al. 1998, García et al. 2006) may be due to the time elapsed since fields were ploughed, which probably influences prey availability. The preference for areas with short vegetation may also explain the reported preferences for stubble over unharvested cereal (Donazar et al. 1993), which was also found in our study (wheat during the nestling period is primarily in the form of stubble), and grazed fallow over ungrazed fallow (Franco et al. 2004). Nonetheless, this selection is obviously mediated by prey availability and kestrels will balance prey abundance with accessibility for foraging habitat selection (optimal foraging theory, e.g. Krebs and Davis 1993). The marked changes found in the Lesser Kestrel’s diet throughout the breeding season (Rodriguez et al. 2010), which primarily relate to prey availability, may also be influenced by the succession of different land-uses that are selected for hunting during different periods of the breeding cycle. In a highly dynamic environment such as the farmed landscape, a particular crop may be very suitable for foraging in March, but not suitable at all in May. Simultaneously, prey items dramatically change in both abundance and composition during the breeding period (Rodriguez et al. 2010). The combined effects of prey dynamism and crop phenology determine foraging success. The Lesser Kestrel has proved to be sensitive to this high dynamism, as documented for other farmland birds (Poole 2005, Trierweiler 2010), changing their perception of the landscape while crops develop. In spite of this, human-based categorization of the farmed landscape by using crop-types is frequent in the literature, probably masking more quantifiable relationships between vegetation structure and farmland bird selection that makes it difficult to generalize results to areas of different land-use composition (but see Serrano and Astrain 2005, Morales et al. 2008). For this reason, we encourage further studies on foraging habitat preferences by farmland birds to consider phenological variations in the impact of land-uses on the foraging of farmland bird species, as well as structural measures of habitat, that will help establish management recommendations for wider geographical areas and/or bigger assemblages of farmland bird species.

Regarding Lesser Kestrel habitat management, this species has demonstrated the ability to survive in areas with very different crop composition (e.g. Donazar et al. 1993, Tella et al. 1998, Franco et al. 2004, García et al. 2006), and recently, it has been suggested that the predominant land use around kestrel colonies should be fallows (Catry et al. 2012b). Although agricultural intensification in our study area is quite low, our conclusions are not necessarily valid for the few pseudo-steppes remaining in Western Europe (Franco et al. 2004, Tella et al. 1998) where the traditional farming system based on the rotation of cereal fields and fallows benefits the species.

Nonetheless, a sizable part of Lesser Kestrel populations live in areas of higher agricultural intensification where a heterogeneous farmed landscape composed of arable crops with different phenologies probably benefits these birds by providing both access to areas of low vegetation cover and height during the whole breeding season and the presence of field margins where prey find refuge. Agricultural activities like ploughing and harvesting may have a facilitation effect on the access to prey, which has been previously documented (Aparicio 1990) and should be studied further. Crop heterogeneity around the colonies allows this facilitation to take place during the whole breeding season, but due to the generalized high selectivity of stubbles during the critical nestling period, sequential harvesting of cereal fields would extend this facilitation (Catry et al. 2012b, see also Johst et al 2001), probably enhancing foraging and breeding conditions for kestrels.

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Table 1. Availability vs. hunting use by Lesser Kestrels (frequency of contacts) and Savage Selectivity Index (Wi) of the different habitats in the three phenological periods. Availability was defined on the basis of temporal land-use information gathered monthly by transects, and calculated for 250 x 250 m cells. Threshold for significance (0.05) was corrected to 0.01, 0.008 and 0.007 for courtship, incubation and nestling periods, respectively, as a result of multiple comparisons. “Others” groups other habitats were kestrels were not found and with availability > 2% such as linear elements, fruit trees, built-up, forests, olive groves and sown fields.

Period	**Habitat type**	**Frequency**	**Availability**	**SSI (Wi)**	**Se (Wi)**	**Chi**	**P**
Courtship							
	Ploughed	28	0.15	3.00	0.3	44.19	*
	Wheat	22	0.27	1.33	0.21	2.49	NS
	Sunflower	7	0.08	1.48	0.44	1.18	NS
	Fallow	3	0.09	0.56	0.41	1.12	NS
	Beetroot	1	0.04	0.42	0.64	0.82	NS
	Others	0	0.25	-	-	-	-
Incubation							
	Sunflower	11	0.16	2.33	0.42	9.96	*
	Ploughed	6	0.04	5.11	0.9	20.66	*
	Fallow	6	0.08	2.54	0.62	6.11	NS
	Wheat	4	0.27	0.51	0.3	2.59	NS
	Cotton	3	0.03	3.64	1.09	5.92	NS
	Beetroot	2	0.04	1.78	0.93	0.71	NS
	Others	0	0.25	-	-	-	-
Nestling							
	Wheat	56	0.27	2.32	0.17	57.90	*
	Sunflower	17	0.17	1.15	0.24	0.41	NS
	Cotton	17	0.06	3.19	0.42	27.25	*
	Beetroot	7	0.01	8.46	1.09	46.46	*
	Ploughed	6	0.07	0.96	0.39	0.01	NS
	Fallow	3	0.07	0.47	0.38	1.88	NS
	Unproductive	1	0.02	0.61	0.77	0.26	NS
	Others	0	0.25	-	-	-	-

Table 2. Parameter estimates of GLMM on strikes considering vegetation cover either as a continuous variable (model 1) or as a binary variable (model 2). Other alternative models explored are presented in table S9.

Model	Variable	Parameter estimate	SE	Chi	P	AIC	AICw
1	Intercept	-0.397	0.18			563.7	8%
	Vegetation height	-0.009	0.003	7.0	0.008		
	Vegetation cover	0.16	0.09	3.5	0.06		
2	Intercept	-0.644	0.22			558.9	92%
	Vegetation height	-0.009	0.003	9.7	0.002		
	Vegetation cover (bare ground)	Aliased	0.29	8.3	0.004		
	Vegetation cover (vegetated)	0.83					

Table 3. Estimates of GLMM on strike success considering agricultural land-use as a binary variable distinguishing whether or not strikes were made in field margins. Other alternative models explored are presented in table S10.

Variable	Levels	Parameter estimate	SE	Chi	P
Intercept		16.53	3109.02		
Phenology	Courtship	Aliased		14.7	0.0007
	Incubation	2.2	0.7		
	Nestling	1.5	0.5		
Field margin	Yes	Aliased		3.0	0.08
	No	-16.8	3109.02		
Harvesting/ploughing		16.9	2651.3	4.3	0.04

Figure legends

Figure 1. Schematic representation of main crop types and kestrel phenology in the study area. Vertical lines represent the development in height of the crop and its drying up process (grey lines). Broken base-lines indicate ploughing and dotted base-lines indicate sowing.

Figure 2. Transects (heavy lines) used to sample Lesser Kestrel foraging behaviours with a 700 m buffer along both sides. The village of La Palma del Condado is delineated in the centre of the image. A North-oriented NDVI image of the area on 5 May 2007 is used as background (Landsat 7 ETM+), and a 250 x 250 m grid is overlaid.

Figure 3. Schematic representation of the hierarchical structure of the analysis for accumulated use.

Figure 4. Mean partial effect of each predictor in the models for Lesser Kestrel presence. Plot a corresponds to the stepwise modelling strategy starting from linear terms and plot b corresponds to the strategy starting from the 3 d.f. spline model (see methods). FFV and BWU are grouping variables considering cover of forested areas, fruit orchards and vineyards, and built-up, water, and unproductive land, respectively. Broken lines indicate the S.E. of the mean. The rug-plot on the x-axes indicates the density of data-points.

Fig1.

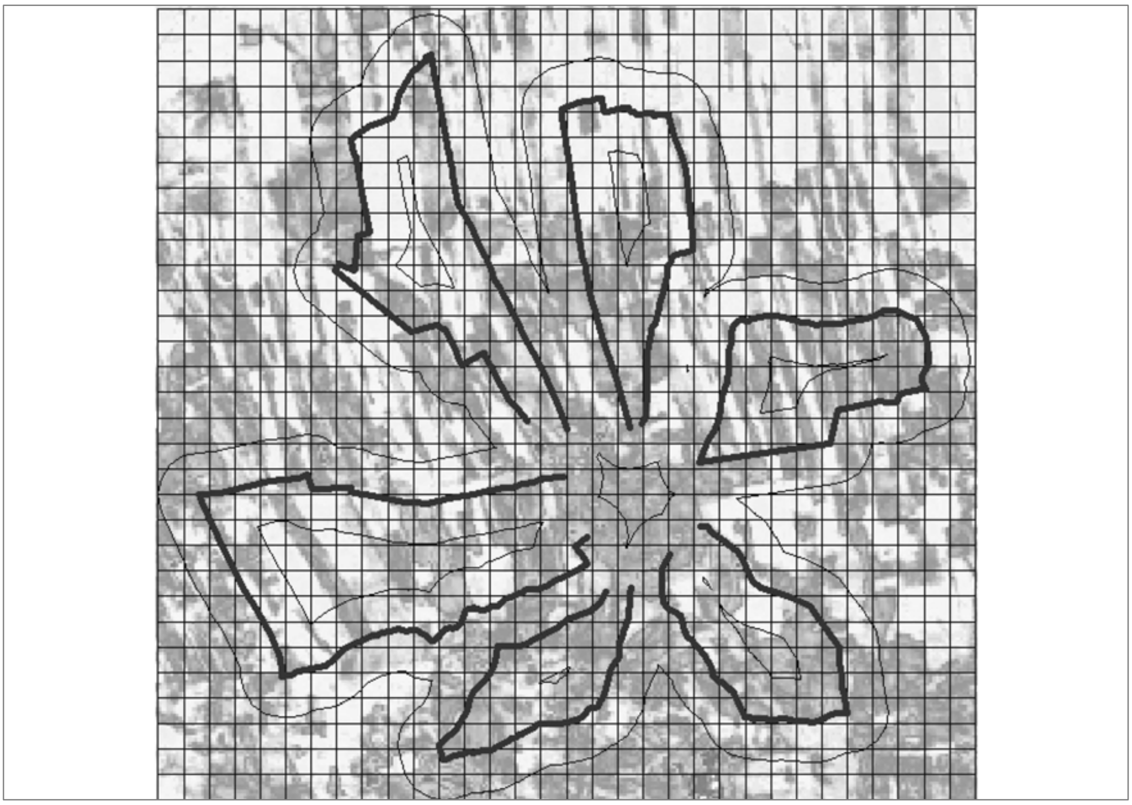


Figure 2.

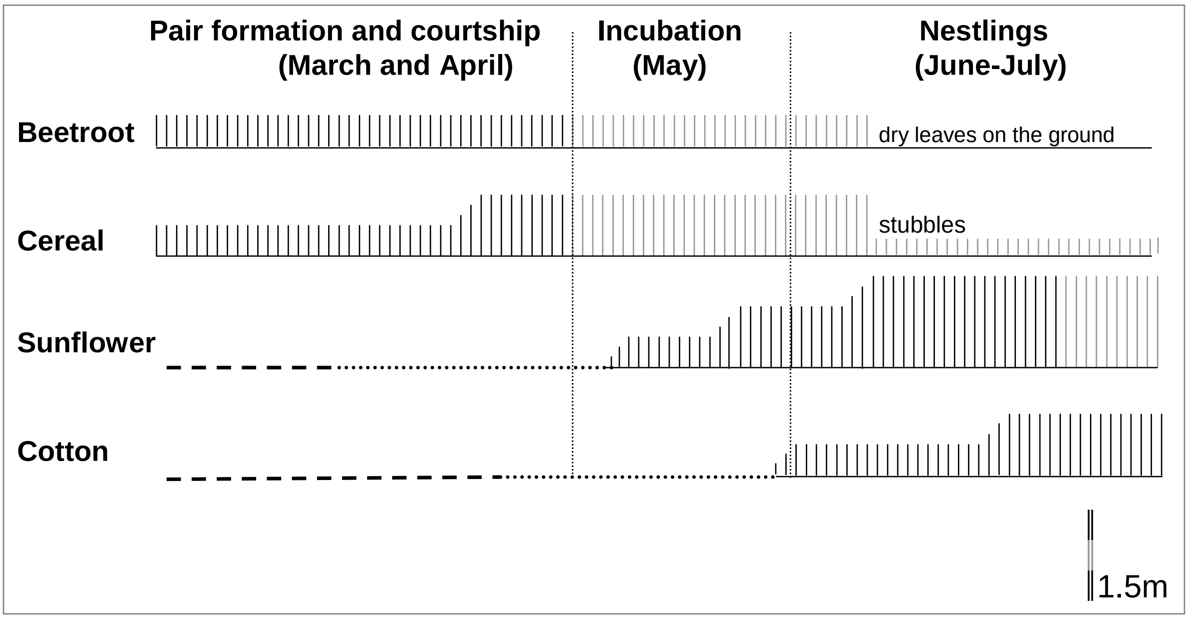


Figure 3

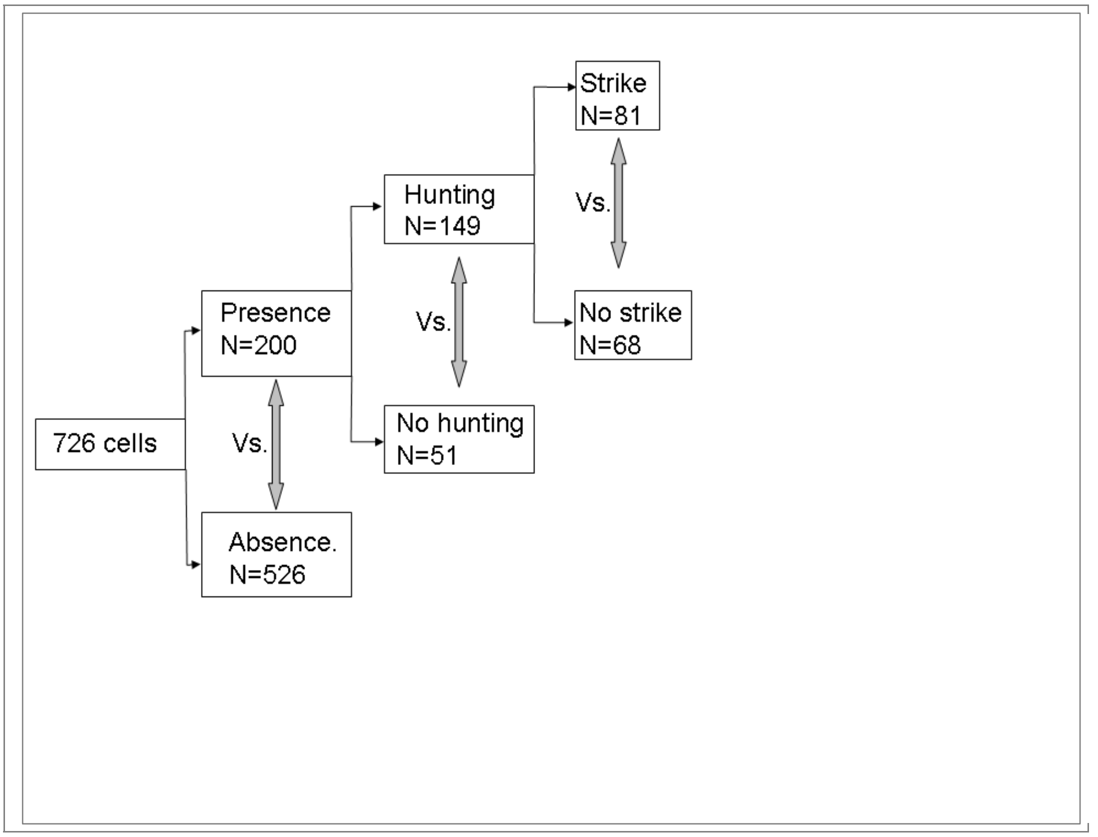
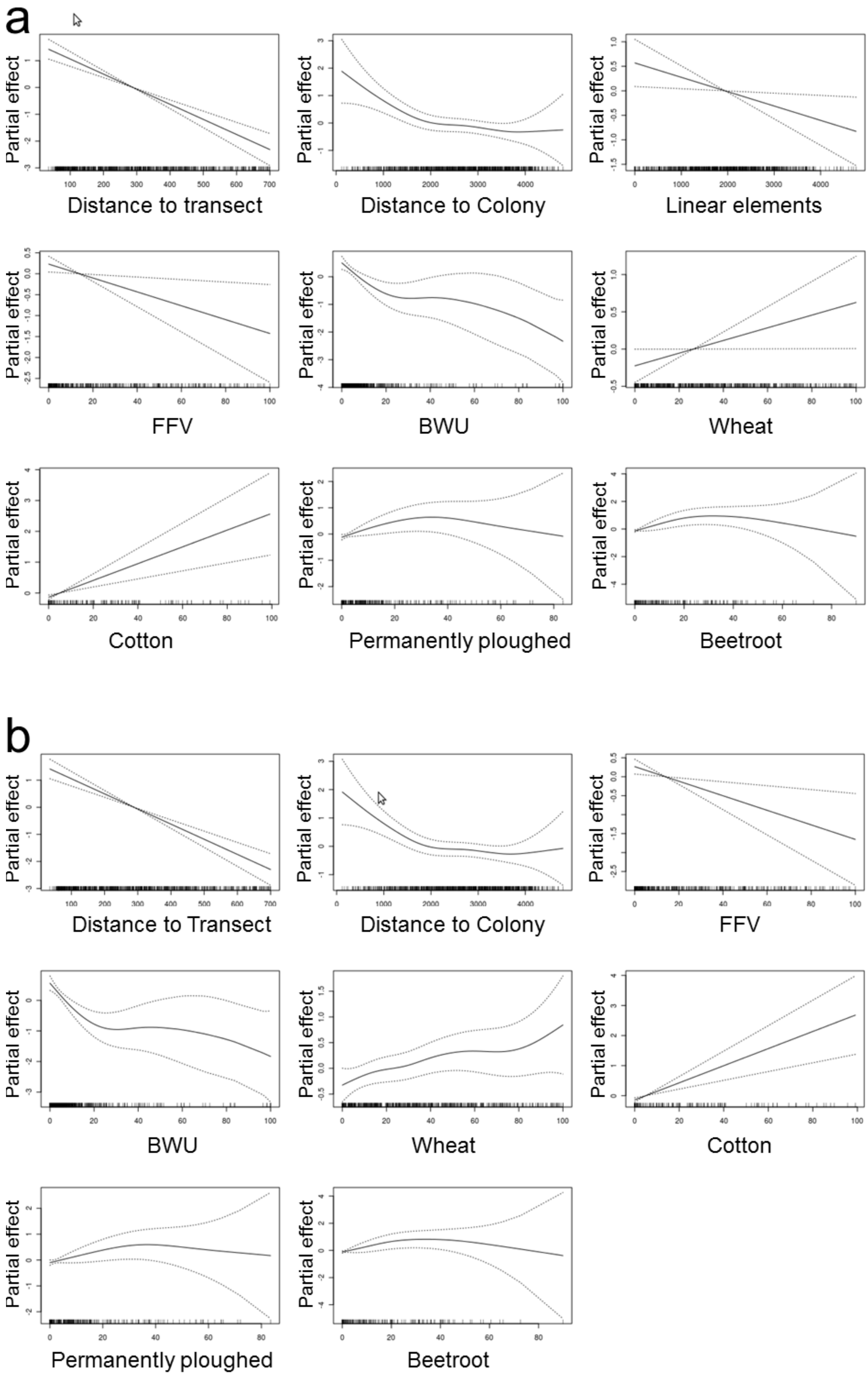

726 cells
Presence
N=200
Absence.
N=526
Vs.
Hunting
N=149
No hunting
N=51
Vs.
Strike
N=81
No strike
N=68
Vs.

Figure 4.


a
Partial effect
Distance to transect
Distance to Colony
Linear elements
FFV
BWU
Wheat
Cotton
Permanently ploughed
Beetroot
b
Distance to Transect
Distance to Colony
FFV
BWU
Wheat
Cotton
Permanently ploughed
Beetroot